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THE POSTGLACIAL DISPERSAL OF THE NORTH AMERICAN BIOTA.¹

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I. INTRODUCTION.

During the last few decades there has been a remarkable accumulation of data on the geographical distribution of the extra-tropical North American biota. In addition to the facts themselves there has been a great advance in those allied sciences which throw some of the most important side lights upon distributional problems—the physiographic and geographic histories of definite areas.

It is of interest to know that the leading factors in this increase in our data have been the surveys by our National Government, especially the work of the U. S. Biological Survey, State Surveys and the great activity of our larger museums, although specialists and amateurs must not be overlooked.

While among many groups there have been notable advances, yet for others our knowledge remains very incomplete, and must apparently remain so because of the immensity of the field and the scarcity of workers. Here even the preliminary organization of data is yet to be made. The recent advance then in distribu-

¹ Read at the Eighth International Geographic Congress, Washington, September 9, 1904.

tional work has been largely due to the great increase in the amount of data.

The next general step of advance which we may expect to follow this stage of rapid accumulation of facts is that of their explanation or interpretation. At present this phase of the subject is much confused by the babel of opinions as to the relative importance of various influences controlling distribution. There are several points of view, and each worker is keen to the influence of certain factors. It is to be hoped that this diversity of opinion will lead to a period of discussion, enriched by many suggestions and discoveries of relations, previously unnoticed. Such a period would certainly hasten the correlation and interpretation of much miscellaneous and imperfectly organized data.

It is to one phase of the subject of faunal interpretation, and the dynamic aspect of the historic factor in particular, to which special attention is directed in this paper. That the historic factor is a real one is very generally recognized, and yet in spite of this fact it is difficult to fully realize that the present distribution which we see, is largely an *effect* of past conditions; the cumulative result of many factors, and not controlled altogether by the conditions of the present environment. To properly estimate this factor it becomes necessary to reconstruct the successional relation and the past conditions, and thus see how each stage has prepared the way for the following one. We must reconstruct the past, for this is as essential in geographical distribution as is the restoration, in the mind of the paleontologist, of the soft parts of the fossils he wishes to interpret.

Some phases of this subject are much more simple than others, just as the history of one region may be much simpler than another. From the biological standpoint this is certainly the case with that part of North America repopulated during the decline of the Wisconsin ice sheet.

To fully understand the return movement to the glaciated region, it is necessary to know the time relations of the various Pleistocene deposits of fossils, as during that time there flourished a variety of forms no longer members of our present fauna. The mastodon, mammoth, peccary, camels, tapirs, native horses and many other forms were then abundant. But, as this phase of

the subject is unfortunately in a very chaotic state little help can come from this source at present. Yet there are certain facts derived from these fossils which are very significant. For example, the occurrence in Pleistocene times (Hay, '02; Hatcher, '02) of such arctic types as the walrus in Virginia and South Carolina along the Atlantic coast, the musk ox in Pennsylvania, West Virginia, Kentucky, Indian Territory and Iowa, and the reindeer in New Jersey, Pennsylvania, Kentucky and Iowa, certainly shows that an arctic climate once reached far to the south. Although limited, this information clearly suggests the general extreme southern limit reached by the arctic types during the Ice Age. As the Wisconsin Ice Sheet was not the maximum one in southern extension, these arctic types, in their last migration in all probability, did not start from this extreme southern limit, but to the north of it. This gives us an approximate starting point in eastern North America of the Postglacial return of life to the glaciated region. From the Great Plains westward the ice sheet did not extend far to the south in the United States so that the return movement in that region began much farther to the north, near the Canadian boundary. At present, as has been said, paleontological facts do not greatly aid in understanding the early Postglacial northward extension of the biota. But there is another source of information to which we may appeal and that is to the affinities or relationships of the biota south of the ice margin. This makes it necessary to take into account the general conditions of life in North America south of the Wisconsin ice margin, and hence to the areas of preservation which must have existed in North America during the Ice Age.

2. BIOTIC PRESERVES DURING THE ICE AGE.

Repeated glaciation had almost sterilized the northern part of the continent. From whence then came the life now occupying that region? Many of the problems involved in a reply to this question cannot be answered at present, but others may be, in an approximate manner. Much exploration remains to be done in northern Asia before we can hope to answer certain questions on those elements in our fauna and flora which have decided Asiatic affinities. But when we consider the more characteristic

American elements, a much greater degree of definiteness may be secured. From our knowledge of the distribution and conditions of life of the present biota, it seems that while the northern part of the continent lay deeply buried under the mantle of the Wisconsin ice sheet there existed, in all probability, south of the ice margin three distinct belts of life (Adams, '02, *b*). At or near the ice margin, and perhaps only forming a narrow transcontinental belt, was the tundra or barren ground biota. Below this first came stunted trees and shrubs, and farther back coniferous forests forming a transcontinental belt, but composed of two distinct types, an eastern and a western one. Below this, in turn, came a third belt of still less homogeneity; in the east it was composed of deciduous forests and their associated fauna, while in the west it was made up of plains and desert types of life.

With these conditions in mind let us now turn to a more detailed consideration of the various elements which go to make up these belts of life, and attempt to follow some of the dynamic phases which this biota has shown since Glacial times. The fundamental idea in following these dynamic changes is that we have belts of physical conditions migrating to the north. Thus there has been given a definite trend to the environment. This fact cannot receive too much emphasis. Just as when studying the littoral fauna of a pond or lake it becomes necessary to bear in mind the dynamic tendency of this littoral zone—that is for it to move inward toward the deeper water—so in a similar manner, to understand the dynamic changes in life areas or zones we must bear in mind the dynamic tendencies in such areas (Adams, '02, *a*, p. 126). Nor is this limited to climatic and topographic influences alone; it includes organic factors as well. It is also necessary to keep such dynamic tendencies in mind when attempting to follow the relations and movements of these three belts in their Postglacial migrations.

The three belts or waves just mentioned were composed of such distinct elements and have had such varied histories that they demand separate treatment. The wanderings of these different types, since Glacial times, is likely to make the application of geographic names confusing (Fig. 1). The members of the

first zone or wave (tundral type) have spread from the Ohio valley to the Arctic sea, the members of the second wave have moved from much the same southern limit to Hudson Bay, but

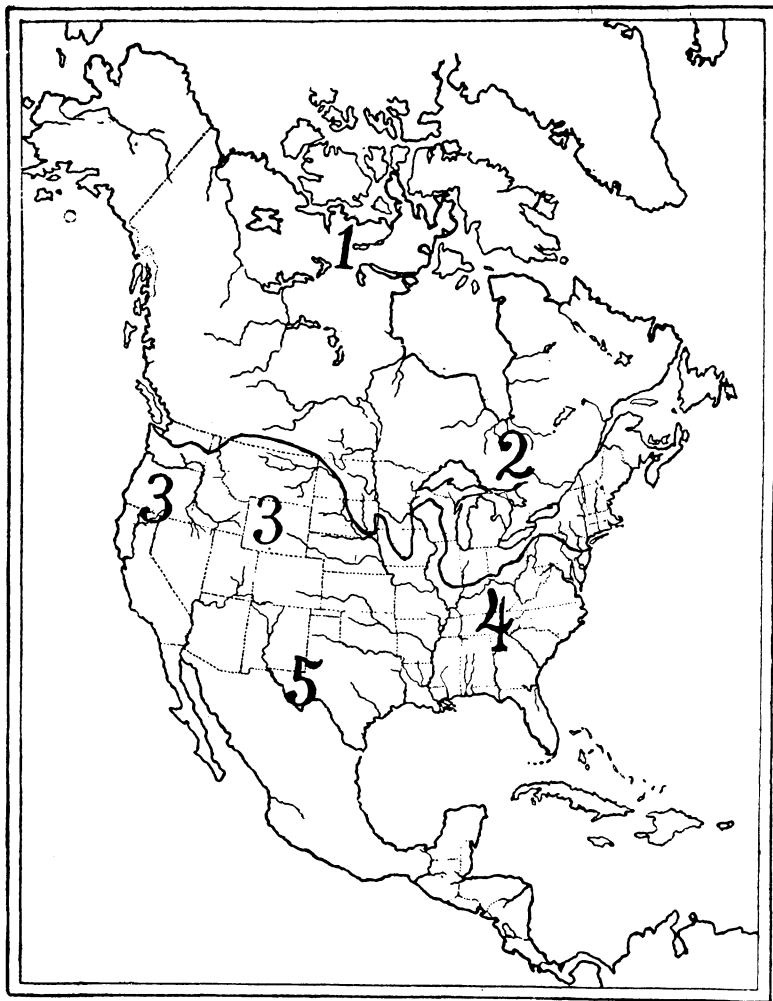


FIG. 1. Showing the present location of the five biotic types and the area invaded by them in Postglacial times. The transverse lines indicates the southern margin of the last (Wisconsin) ice sheet.

the third wave, composed of the southeastern and southwestern biota, has been relatively stationary. The first two waves entered the territory they now occupy largely from the *south*, although

we usually think of them as completely boreal forms and tending southward in their dispersal. Turning now to a brief consideration of the primary characteristics of these elements in the biota and beginning with the one which invaded the glaciated region first we have the following order of succession :

First Wave.

1. *Tundral or Barren Ground Biota.* — This element of the return movement exists to-day in the north beyond the tree limit and as relicts farther south upon mountain summits. This is a circumpolar type and has little peculiarly American. Its original center of dispersal may have been farther south near the centers of ice accumulation, or as Dixon ('95, p. 298) has suggested in the elevated regions of the tropics. In either case it has had a very nomadic existence.

As there is reason to believe that the ice did not completely cover all the northern land some of this type flourished there, in all probability, even in Glacial times, as for example, in the Point Barrow region of Alaska, where Nelson ('87, p. 27) has noted the distinctly Siberian affinities of the biota. This factor suggests that the life of this region is an overflow perhaps in preglacial or Glacial times from unglaciated Arctic Siberia.

Migration and Dispersal Routes. — The first wave biota has apparently reached its present location by a northward Glacial and Postglacial migration, and has been supplemented by certain Glacial relicts, from Alaska in particular, as has been suggested, while in more recent times some additions have been received from Asia and Greenland as has been shown by Stejneger for the wheatear ('01, *a* and *b*). The migration route of the western birds of this species points to India by way of Alaska, and the eastern ones to Africa by way of Greenland.

Probably the latest paths followed northward were along the mountain chains, where occasionally colonies have lingered, in favorable conditions, upon mountain peaks.

Second Wave.

2. *Northeastern Biota.* — The second wave was of the biotic type now represented by the northern transcontinental coniferous

forest belt. But this belt was not homogeneous from east to west and the eastern element in this wave will be considered first. On account of its wanderings, this wave as in the case of the first cannot be geographically defined in the east as a center of dispersal, without danger of confusion. Although this biota reaches its best development at the present time, in the northeast, yet it is only a relatively late arrival in that region. For eastern North America this was the "second wave" (Adams, '02, *b*, p. 309) to pass north after the retreating arctic climate attending the decline of the Wisconsin ice sheet. The region now occupied by this biota is an area with abundant lakes, peat bogs and a region of poor drainage. The area is covered by coniferous forests but it is of a very different type from that found in the Rocky Mountain region as has been shown by Rydberg ('00, pp. 871-873). Here the very characteristic bog plant society reaches its best development as shown by Transeau ('04). This is the region of fur-bearing animals, and there are very few reptiles and amphibians. On the west this biota swings north of the Great Plains in Canada to the Rocky Mountains and then north into the Mackenzie basin.

Migration and Dispersal Routes.—The northeastern type of biota has moved from about the latitude of the Ohio valley north to its present position. Certain elements have apparently pushed far northwest to the Rocky Mountains, to the Mackenzie basin, and even overflowed into the Yukon valley—the reverse route, in all probability, was followed by certain Asiatic forms into America. This westward and northwestward dispersal has tended perhaps to overemphasize the transcontinental distribution of these northern types and shows how the determination of faunal areas based primarily upon the present conditions tends to obscure the compositeness and diversity of origin of their constituent elements. This biota reaches its greatest southward extension along the Appalachian Mountains. Laggards of this and the barren ground type form the "boreal" islands, when surrounded by the life of the following wave. These occur not only upon mountain tops, in bogs and on sand dunes but also in certain deep lakes, where the "abyssal" fauna shows very decided northern affinities, and clearly suggests them as Glacial relicts.

3. *Western Center of Dispersal*. — In the West we recognize a second center of northward migration. It is represented by the biota of the Rocky Mountains and the Pacific coast region. Its great extent, even in Glacial times, south of the ice margin and its present occupation of the field, allows this biota to be geographically defined as the Western Center of Dispersal. In contrast with the region dominated by the eastern part of this wave the western branch occupied a high mountain country. It was a coniferous forest belt, but as has been mentioned, was of a very different type from that of the northeast. The present flora of the Rocky Mountains and the coast region is of the same general type, as shown by Coville ('93, pp. 29-31) and Rydberg ('00, p. 871), although the climatic conditions are quite different in several respects. It should also be recalled that much of the recent botanical work has been done in the Rocky Mountains near the Canadian border so that later studies in the southern Rockies may, to some degree, lessen this apparent uniformity. These facts do not favor the idea of transcontinental unity of the coniferous forests but show that the direction of geographic origin, the adaptations of the biota to mountain conditions, and proximity, are factors which must be reckoned with in understanding the Postglacial repopulation of the Northwest. The same factors also suggest that the usually accepted transcontinental distribution of the fauna may be overestimated. At least it is very evident that many of the characteristic animals of the western mountains are lacking in the relatively low eastern Appalachians. Such a relation may have been closer in the past than it is at present, as is suggested by the occurrence of the pica (*Ochotona*) in the Pleistocene of Pennsylvania, although now, in North America, it occurs only in the western mountains. There is also in the West a great increase of Asiatic types, in addition to certain native elements. The mountain goat (*Oreamnus*) and big horn (*Ovis*) are representative mountain forms of the west but lacking, even as fossils, in the east. Among some invertebrates this is also true, as for example, the butterfly genus *Parnassius*, the crawfish *Potamobius*, the west coast *Unionidae* and certain *Arionta*-like land shells, are quite distinct from eastern types. The composition and affinities of this western biota

require much more study before its true position can be determined. In marked contrast with the northeastern biota this one has long been bounded on the south and east by an arid climate.

Migration and Dispersal Routes.— With the exception perhaps of Glacial relict colonies in favorable spots along the Pacific coast, and in the unglaciated parts of Alaska, the biota of the Pacific coast and Canadian Rockies must have pushed into this region primarily from two directions in Postglacial times. To a limited extent there was an overflow of the northeastern biota but the great bulk of the population came from the Rocky Mountains and Pacific coast region south of the Canadian border. Dispersal must have been carried on under great disadvantages, on account of the topographic difficulties. But this biota, on account of its proximity, and early invasion of the region, had manifest advantages over the later arrivals. That a great wave of life moved north along the mountains from this western center is very apparent from the present affinities of the life of the region extending from southern British Columbia to Alaska. The primary highways were probably the mountains themselves, and a narrow coastal strip, now largely submerged. These lines of dispersal are today migration routes for birds. Bishop ('00, p. 50) has shown that a large part of the Yukon valley birds winter in western United States, and this clearly suggests their western origin.

The extensive distribution of certain forms in northwest North America, and their occurrence as well in the northeast, has suggested the northwestern origin of such forms. From the present standpoint it seems more likely that most of these northwestern forms have been derived from the western center of dispersal from which they spread north or later overflowed into the northeast. It also seems that the northern biota in general has had a northern rather than a southern trend to its dispersal.

The Alaskan region, in addition to its Glacial relicts, was apparently repopulated in part by a northward invasion from the western center of dispersal along the mountains, by a double invasion from Asia (Stejneger) north and south of the Stanovoj Mountains, and by contributions from the northeastern biota.

It also appears that some of the mountain biota of the Canadian Rockies were driven north into unglaciated Alaska as the ice spread from the Cordilleran center of ice accumulation.

Third Wave.

4. *Southeastern Center of Dispersal.*—The region occupied by the southeastern type of biota was largely south of the territory invaded by the ice, and its biota has therefore been relatively stable in its geographic position when compared with the extensive migrations of the first and second waves. As today, during Glacial times, this biota was bounded on the west by the arid plains. This is a region of low plains and plateaus, the higher mountains within this area still retaining the second wave types as Glacial relicts. It is probable that the first wave type never reached in abundance so far south. The climate of this southeastern center is equable and there is abundant rainfall. The dense deciduous forests furnish favorable conditions for animal life. This region has not only been important as a region of preservation, but also as a center of origin. Here there is the best development of the deciduous forest and the most characteristic features of the land and fresh water shell life of North America. This has also been the center of distribution of several vertebrate types and also for certain plants. But as this center has been discussed elsewhere (Adams, '02, a) only brief mention will be made here of its characteristic features.

Migration and Dispersal Routes.—With the retreat of the ice this biota formed the eastern element of the third wave. It moved north and northwest behind the coniferous forest zone. But as this biota was relatively stable its center of dispersal can be definitely defined as occupying southeastern United States, east of the Great Plains. This stability therefore makes the dispersal routes of more importance than the migrations of the biota as a whole, as the spread of this biota has apparently been influenced more by the normal increase of a populated area than by a great change in the physical conditions which was such a dominant factor farther north.

The primary routes for the land forms were the Coastal Plain and its valleys, the Appalachian plateaus, and the Mississippi

and tributary valleys. For the aquatic types the Tennessee and Mississippi Rivers were the leading highways. From the upper end of the Coastal Plain a limited number of land forms pushed up the Hudson and even worked west via the Mohawk valley to the Great Lake region. From the Mississippi numerous tributary valleys were followed, the Ohio, Wabash, Illinois, and Missouri, and thus this biota radiated rapidly. It even invaded the Great Plains along eastward flowing streams, especially along the Missouri River.

The second wave types reach their most southern extension along mountains while this third wave reaches its most northern extension along valleys, not only to the north but also upon the arid plains of the northwest.

5. *The Southwestern Center of Dispersal.* — The area occupied by the southwestern biota was largely far beyond the ice margin and, like that of the southeastern, was relatively stable in its geographic position. At present this type is represented by the life of the arid southwest, including the Great Plains, the Great Basin, the central valley of California and the Mexican Plateau. It is a vast region of arid plains, desert plateaus, and mountains, subject to great climatic extremes. In spite of the severity of the conditions of life the biota is quite varied, and many kinds are abundant. Attention has already been called (Adams, '02, *b*, p. 121) to the importance of this center and too much emphasis cannot be placed upon its importance, not only as a center of distribution, but also as the region of origin of the arid North American biota. It seems equally evident that before a reliable estimate can be made of this biota it must be carefully compared with that of the arid regions of South America and of Asia. The life of the first and second waves in the Postglacial migrations contained many forms not peculiarly American, but the southeastern and southwestern elements of the third wave show much more individuality. The southeastern center has certain endemic elements in its flora and fauna, yet several other types have their affinities duplicated in eastern Asia, and thus its individuality is somewhat lessened. On the other hand the southwestern center, although it shows some Asiatic duplication, does not appear to be so marked. So far as known to me no one has

made a detailed comparison of the arid types of the two continents.

The distinctness of the southeastern and the southwestern centers is frequently overlooked or confused. And this is especially liable to be the case when allowance is not made for the influence of local conditions upon the occurrence of certain southwestern types which have overflowed into the eastern center. This brings up the following question, which as will be seen later on, clearly emphasizes the importance of habitat study in geographical distribution. In estimating biotic areas, how much weight should be given to the occurrence of forms dependent upon limited local conditions? A bare census gives no idea of the relative weight of the units recorded or the degree of representativeness of them. The importance of such a study in a proper estimate of local conditions has been suggested repeatedly in attempting to determine the relations of these two centers. These relations have suggested that perhaps biotic affinities can be more easily and safely determined by habitat and biotic associations than primarily upon a faunistic or floristic basis. This would mean that the ecological relations rather than the taxonomic affinities should receive greater attention than is customary. It should be noted, however, that this view does not in any way belittle the importance of taxonomic work in distributional studies. But it is sufficient, at this place, simply to call attention to the ecological aspect of the subject.

But to return to the consideration of the southwest, the vegetation of this arid region is composed of grasses on the plains, and cacti, agave, yucca, and many other types of desert vegetation in the more arid places. Reference need only be made to the recent paper of Coville and MacDougal ('03) for the characteristic features and the literature on this flora. The fauna is equally peculiar and interesting. This is the region where prairie dogs, spermophiles, pocket gophers, pocket mice, wood rats, kangaroo rats are so characteristic, and the horned toads, rattlesnakes and many other reptiles reach their greatest variety and center of abundance. This has been the center for many other forms as well. Certain crawfishes (Ortmann, '02) have originated here. Many groups of insects are also characteristic. The bees of the genus

Perdita are very abundant, and as Prof. T. D. A. Cockerell informs me, are very characteristic, only a few species occurring east of the Great Plains (Cockerell, '98). The beetles of the family *Tenebrionidæ* are quite abundant. The ant-lions, *Myrmeleonidæ*, here reach their greatest development in variety and abundance. The fish fauna is limited and peculiar; those of the Rio Grande have Mississippi River affinities, while those of the Colorado River show much endemism, as shown by Meek ('03). Of its 32 species, only 10 are known to occur elsewhere.

Migration and Dispersal Routes. — As only a small part of this southwestern center was invaded by the Glacial ice its geographic position has been relatively stationary. Since the Ice Age, however, there has been considerable overflow to the north. Starting in the southwest this biota has been spread northward along each side of the Rocky Mountains, and has invaded an arid region, a condition to which it was evidently well adapted. Even glaciated portions of British America were reached on each side of the mountains by these hardy forms of life.

Other plants and animals have spread from here into the southeast, where on account of its varied conditions of life they have been able to flourish. This, for example, is seen in the case of yucca, lizards, and pocket gophers. These forms have been able to find favorable arid *local* conditions in the southeast, as in the pine barrens and on dry hillsides, etc.

These arid types find their eastern extensions upon the dry uplands interdigitating with the southeastern types which frequent the moist valleys. They reach their extreme eastern extension, in abundance and in association, upon the prairies of Wisconsin, Illinois, and northern Indiana. But with the clearing away of the forests this eastward advance has been greatly hastened.

The aquatic life of this center has communicated with the Mississippi River, as shown by the Rio Grande fish fauna, but that of the Colorado River has been isolated to an exceptional degree, and has developed a remarkable individuality.

3. SOME FACTORS IN BIOTIC INTERPRETATION.

In a previous paper (Adams, '01) the writer has discussed the relation of the baseleveling processes upon habitat differentiation

and their influence upon the successional relation of the faunas correlated with the degree of topographic development of a region. Although the fauna was mentioned in particular, these factors influence the entire biota in a similar manner. During the process of degradation of the land there is a definite and orderly succession of conditions through which the habitats pass; the brooks become larger streams, the lakes and ponds become drained, and the uplands are lowered, etc. Not only does the location of the habitats change but also their relative positions and extent. On account of the great influence which topographic conditions have upon habitats it is possible to find very diverse biotic conditions even in a relatively small area. Students of local faunas and floras frequently comment upon this diversity, and although these facts are often noted, yet but little attention is given to them because of their seeming chaos. This apparent mixture or confusion is often due to a total disregard of the habitats and the associations of the forms in them. That this occurrence is, as a rule, quite definite and orderly, may be seen by reference to the example of certain southeastern types evidently of western or southwestern origin, the yuccas and pocket gophers. These are types from an arid region, and it is important to note that when they invade a moist region they occupy the relatively dry situations — the pine barrens, sandy or rocky places — for such are the conditions most nearly approaching their original home. Such colonies form "islands" of arid types surrounded by those correlated with greater moisture. The significant fact here is the definiteness of the conditions in which they occur. Again this same tendency is shown in the extreme northward extension of the southeastern biota along protected valleys, and even far out upon the Great Plains. Similarly in southern Michigan, certain characteristic members of the southeastern biota enter the state at the southeastern and southwestern corners, rather than along the southern border, because valley highways enter the state at these corners. Apparently this same route into southeastern Michigan has been utilized by certain forest trees, insects, birds and doubtless other southern types, which have also invaded extreme southwestern Ontario. Such facts might be indefinitely multiplied, but these clearly show that

invading *elements tend to enter a region, not only at a definite place, but also tend to remain in definite habitat associations and conditions even after having once entered a region.* This habitat individuality causes more or less isolation of the various elements invading a region and furnishes an index to their direction of origin, and at the same time reinforces the idea of the regularity of their field relations. To be sure this definiteness becomes more or less blurred and indefinite along tension lines, but it is not confusing when considered with the proper perspective.

It is quite evident that the kinds of biota frequenting similar habitats must be largely different in distinct biotic regions. This may be seen by a comparison of the same habitats in regions occupied by distinct biotic types. Thus if a comparison is made between the shell life frequenting the margin of an isolated pond in Michigan and that occupying the similar habitat of a sink hole pond in east Tennessee, a marked dissimilarity is noticed. In the northern pond there will be an abundance of shells belonging to the genera *Limnæa* and *Physa*, while in the southern one these genera will be poorly represented or entirely absent. If a similar comparison is made between the shells found in rapidly flowing brooks, from the same regions, the southern stream will abound in shells of the family Pleuroceridæ, a family poorly represented in the north. The Limnæidæ are northern in their distribution, and the Pleuroceridæ are characteristically southeastern. The same general relations hold for the vegetation; in the southeast there is the deciduous forest and in the northeast a coniferous one.

On account of the unique character of the life occupying the same kind of habitats in distinct biotic regions, there results, in these regions, a different succession of forms attending changes in the topography, climate or any other factors which may influence habitats. *Thus the succession of ecological associations is likely to be similar, even in very distinct regions when similar processes and conditions are at work, yet the biotic components, the families, genera or species, etc., are likely to be quite different.* Such relations as these mean that from very diverse kinds of life there tends to be formed, *de novo* or by association, certain ecological types which become correlated with certain habitats.

Thus certain habitat types have originated many times independently. For example, the fresh water fauna was not formed all at once. This environment has been independently and repeatedly invaded by very diverse animals and from diverse habitats. The same is equally true of the minor fresh water habitats, such as that of the littoral zone or the rapid water of a brook, etc. The same is equally true of land habitats, such as caves, deserts and many other situations whose biota has been derived from all possible directions. It is thus evident that there are two fairly distinct classes of succession in a given biotic region, the adaptational one, in which the ecological aspect is prominent, and the hereditary one, in which the taxonomic or hereditary aspect receives emphasis.

From the above considerations of habitats and their biota, their successional relations and their convergent habitat and ecological tendencies, we are led to a very natural question: What is their bearing upon migration and dispersal centers? This relation is very close and unfortunately only too often completely overlooked. If in the study of the life of a given region practical recognition can be made of the above mentioned relations, which are involved in the study of the origin of the biota of given habitats, there will result a very desirable *geographic perspective*. Such a perspective will greatly aid in the determination of the relative influence of the factors of the environment. As the habitats of many plants and animals change with geographic range it is very desirable to take advantage of this variation in estimating the relative influence of different elements in the environment. In this way we may hope to distinguish between the local and geographic conditions, influences which are easily confused. It is primarily their reflex effect upon geographic distribution, and especially upon biotic interpretation which interests us at this time, a subject which can not be separated from a consideration of the relative influence of environmental factors. Habitat studies not only throw important light upon geographic origin of biotic elements but also upon the conditions of life determining routes of dispersal, and these are often very important elements in biotic interpretation. For it seems at present that it is along this line that we may expect, in the near future, some of the most rapid advances in distributional problems.

4. SUMMARY AND CONCLUSION.

In summarizing we may note that recent advances made in the study of the extratropical North American fauna and flora have been primarily due to the rapid accumulation of data. In the near future, rapid advances along the line of explanation and interpretation of these facts may be expected. As the present distribution is in part an *effect* it is therefore necessary to take into account certain past conditions. Very important among these factors have been Glacial and Postglacial influences upon this region. These geological changes have had a great influence on the biota, not only on account of the wonderful changes in the physical conditions of life, attending the decline of the Ice Age, but also on account of the definiteness given to the dynamic tendencies by this environment. When attempting to determine the affinities and interrelations of the present biota too much emphasis cannot be placed upon this definite dynamic tendency, and to the sources and routes followed by the life on its return to the glaciated region. This returning biota followed, in all probability, a definite successional relation and was composed of three general belts or "waves," concentrically distributed south of the ice margin. The first one was of the barren ground type, the second was represented by distinct eastern and western coniferous forest types, and the third by the biota of the southeastern and southwestern states. The first wave was of a transcontinental extent, the second while coniferous and transcontinental was composed of two distinct types, the eastern, represented by the biota of northeastern North America, and the western by that of the Rocky Mountains and the Pacific coast. The northeastern biota overflowed to the north, to the northwest into the Mackenzie basin and even a few forms into the Yukon valley and to the Rocky Mountains. The northwestern biota spread from the Rocky Mountains and Pacific coast regions in the United States north to British Columbia and Alaska. The third wave spread from the southeastern center of dispersal northward to the conifers, and west to the Great Plains. From the southwestern center the life spread north on each side of the Rocky Mountains into Canada, and only stragglers spread eastward into the humid southeast.

Further light is to be thrown upon the interpretation of these centers of dispersal and their biotic types by taking into account the successional relation of the biota, as correlated with changes of the environment. The habitat relations of organisms show that they do not occur promiscuously mixed, even within a small area, but that their relations are orderly and definite. In addition to the general successional relation attending changes of the environment, attention is called to the different kinds of organisms in different biotic regions, which make up this succession. This habitat uniqueness of the biota in different regions favors the independent formation or association of similar habitat types from very diverse kinds of biota.

With these sources of Postglacial supply, their routes of dispersal, and their definite habitat relations fresh in mind, it becomes very evident that these factors must greatly influence our interpretation of life areas. These facts strongly suggest that the present conditions of life cannot be expected to fully explain the present distribution, and clearly emphasize that the historical factor must be dynamically considered.

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